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Cumulative and Far-Field Fish Habitat Effects

Effets cumulatifs et à très grande distance sur l'habitat du poisson

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ABSTRACT

Shellfish aquaculture operations have the potential to substantially modify their surrounding environment. They represent a net addition of habitat to coastal systems and may directly and indirectly influence system productivity, nutrient dynamics and ecological rate processes. As a result ecosystem scale effects of shellfish aquaculture are complex and comprehensive studies are limited. In this paper we will discuss the characteristics of coastal ecosystems that are important determinants of the potential for far field or ecosystem scale consequences of shellfish aquaculture. We advance a scaling approach as a useful tool to frame questions about such consequences and briefly discuss existing options for predicting ecosystem scale effects. We end with a review of the cumulative effects of terrestrial agriculture and shellfish aquaculture using Prince Edward Island estuaries as a relevant Canadian example.

RÉSUMÉ

Les exploitations conchylicoles peuvent modifier considérablement leur milieu environnant. Ces exploitations représentent une nette addition d'habitat aux systèmes côtiers et peuvent influencer de façon directe et indirecte la productivité des systèmes, la dynamique des substances nutritives ainsi que le rythme des processus écologiques. En conséquence, les effets de la conchyliculture à l'échelle écosystémique sont complexes et il existe peu d'études approfondies sur le sujet. Dans le présent article, nous examinerons les caractéristiques des écosystèmes côtiers, lesquelles ont une incidence déterminante sur la possibilité que la conchyliculture ait des conséquences sur une échelle écosystémique ou sur une très grande distance. Nous présentons une approche de mise à l'échelle en tant qu'outil utile pour définir des questions plus précises portant sur de telles conséquences et étudions brièvement les options actuelles de prévision des effets à l'échelle écosystémique. Nous terminons avec un examen des effets cumulatifs de l'agriculture terrestre et de la conchyliculture, en utilisant les estuaires de l'Île-du-Prince-Édouard à titre d'exemple pertinent au Canada.

INTRODUCTION

Habitat Management requested science advice on the following questions. How can the cumulative fish habitat effects of shellfish aquaculture (*e.g.* marine eutrophication, oxygen or phytoplankton depletion, community shifts, exceeding carrying capacity) be quantified? Can far-field or ecosystem-scale fish habitat effects of shellfish aquaculture be predicted or measured? If so, what tools or indicators are useful for these purposes?

Shellfish aquaculture operations have the potential to substantially modify their surrounding environment. Unlike intensive finfish farms where a primary environmental concern is the consequence of increased organic matter loading, shellfish farms represent a net addition of habitat to an ecosystem. As well, the addition of suspension feeders can alter seston properties and dynamics and modify the fluxes of material and energy through the ecosystem. If as is frequently the case, substrate is the limiting factor for benthic organisms, the addition of shellfish can substantially increase secondary production of a coastal ecosystem. If on the other hand primary production limits benthic productivity then the addition of suspension feeders may result in foodweb shifts as they compete with other secondary producers and transfer water column primary production to the benthos.

Benthic processes may be responsible for up to half of the nutrient mineralization in estuaries (Heip et al. 1995; Herman et al. 1999; Ysebaert et al. 2002) and benthic production frequently dominates secondary production in estuaries and coastal regions. Yankhe (2006) calculates that benthic primary production represents 1/3 of total primary production in the south Atlantic Bight. Microphytobenthic communities also contribute significantly to denitrification rates in coastal systems (Sundbäck and Graneli 1988). Thus the addition of benthic habitat and additional suspension feeders to a coastal environment will affect not only the flux of seston from the water column to the sediments (as a result of particle repackaging and hydrodynamic regime modification) but also the benthic pelagic coupling and nutrient dynamics (directly by excretion and indirectly by modification of sediment properties). The importance of shellfish as habitat and the consequences of shellfish aquaculture for fish habitat have been reviewed by McKindsey et al. (2006) and the potential environmental effects of shellfish aquaculture operations are presented by Cranford et al. (2006). They will not be repeated here. In this paper we will discuss the characteristics of coastal ecosystems that are important determinants of the potential for far field or ecosystem scale consequences of shellfish aquaculture and will advance a scaling approach as a useful tool to frame questions about such consequences. It must be remembered that, unlike many near-field effects that are fairly well studied and understood, many far-field effects remain only postulates at this time (Broekhuizen et al. 2002), largely as a function of the many complicated ways in which bivalve operates within the ecosystem. That being said, coastal ecosystems are increasingly stressed by many human activities and thus any one such activity should not be considered in isolation. We end with a review of the cumulative

effects of terrestrial agriculture and shellfish aquaculture using Prince Edward Island estuaries as a relevant Canadian example

DEFINITION OF FAR-FIELD IN THE CONTEXT OF SHELLFISH AQUACULTURE

Shellfish are recognized as "ecosystem engineers" because of their ability to form reefs or colonies and to structure and modulate ecosystem functions when present in sufficient numbers (Gili and Coma 1998). Environmental effects of shellfish aquaculture may therefore occur beyond the boundaries of the farm. Thus, regardless of whether shellfish are wild or farmed, they are an integral part of the coastal aquatic ecosystem. As a result, a distinction between "near-field" and "far-field" effects is arbitrary at best. In the context of shellfish aquaculture, the term "far-field" effects can most simply be defined as "the influence of the shellfish on ecosystem processes and structure at some distance from the farm.

Where benthic effects due to increased sedimentation have been demonstrated, most are immediately below or within short distances of the farm (Cranford et al. 2006; Hartstein and Stevens 2005; McKindsey et al. 2006; Miller et al. 2002b). Similarly localized direct (near-field) effects of water column seston depletion (Cranford et al. 2006; McKindsey et al. 2006; Prins et al. 1998) or nutrient enrichment (Cranford et al. 2006; McKindsey et al. 2006; Prins et al. 1998) are demonstrated within the immediate confines of a farm at some sites. The occurrence and magnitude of such effects is dependant upon many factors including the stocking density and bathymetric and hydrological characteristics of the lease.

What may be termed as "near-field" effects may ultimately result in a number of potential "far-field" effects, including increases, decreases or stabilizing of the abundance and/or productivity of a variety of processes and components within ecosystems (nutrients, phytoplankton, zooplankton, benthos, fishes, macroalgae, etc). A good review of potential far-field effects may be found in Broekhuizen et al. (2002), Gibbs (2004), and Jiang and Gibbs (2005) and is expanded upon in Table1.

Table 1. Postulated and demonstrated far-field effects of bivalve culture. Although some effects may normally be considered as "near-field", they may have "far-field" consequences on other components of the ecosystem.

Ecosystem component	Nature of effect	Mechanism and evidence
Hydrodynamics	modified currents	mass of physical structure in hydrodynamic environment[1]
Nutrients	Sediment-related	
	stabilized	phytoplankton blooms ↓ thus variation of flux to benthos reduced[2]
	decreased	↑ denitrification and switch to N_2 production[3]
	increased	↑ ammonium[4], silicon[5], and others[6]
	Δ proportions	biogeochemical pathways altered by increased deposition[7]
	Bivalve-related	
	increased	metabolism increases nutrient release[8]
	decreased	bivalves a sink for organic nitrogen[9]
	stabilized	bivalves may use all varieties of available food sources and continually release nutrients[10]
Phytoplankton	reduced	grazing reduces standing stock[11] sequestration of nutrients in sediments and bivalve tissue reduces primary productivity[12]
	increased	increased net nutrient fluxes (not only phytoplankton metabolized) enhance production[9]
	Δ assemblages	
	toxic blooms	via Δ nutrient ratios[13]
		via introduction of toxic plankton with transfer[14]
	# blooms ↓	via stabilization of nutrient supply and opportunistic bivalve grazing[15]
Zooplankton	reduced	directly via bivalve predation[16]
		indirectly via competition with bivalves[17]
	increased	indirectly via increased stability and abundance of phytoplankton[15]
	Δ assemblages	preferential prey selection by bivalves[18]
		modification of food via bivalve predation[19]
		influx of bivalve larvae in plankton[18]
Eggs and meroplankton	reduced	by grazing[20]

Benthic communities	Δ assemblages	selection for species lacking planktonic stage because of predation by bivalves on eggs-meroplankton[16]
Benthic communities		competition with bivalves for food[21]
		reduction in numbers of propagules available via bivalve predation[20]
		enhanced recruitment of bivalves in surrounding environment with cascading effects on related assemblages[22]
		attraction of mobile organisms to artificial reef structure of bivalve culture: i) diminished abundances outside of farms, ii) diminished abundances in system via enhanced (fishing) mortality in farms[23]
		enhanced productivity of associated species influences surrounding ecosystem[24]
		exotic species introduced with or promoted by bivalve culture[25]
		increased water clarity increase photic zone[26]
	↑ productivity	cascading effect from stabilization of nutrients, phytoplankton, etc[2]
	↓ productivity	cascading effect from Δ to phytoplankton and zooplankton communities[28]

[1]Strohmeier et al. (2005), [2]Dame (1996), [3]Kaspar et al. (1985), [4]Strang (2003), [5]Prins and Smaal (1994), [6]Dame (1996), [7]Newell (2004), [8]Asmus and Asmus (1991), [9](Kaspar et al. 1985), [10]Cranford et al. (2006), [11]Carver and Mallet (1990), [12](Kaspar et al. 1985), [13]Bates et al. (1993), [14]Scarratt et al. (1993), [15]Herman et al. (1990), [16]Wong and Levinton (2006), [17] Prins et al. (1998), [18]Lam-Hoai and Rougier (2001), [19]McKindsey et al. (2006), [20]Gibbs (2004), [21]Dankers and Zuidema (1995), [22]Branch and Steffani (2004), [23](Powers et al. 2003), [24]Inglis and Gust (2003), [25]Landry et al. (2006), [26]Rice (2000), [27](Broekhuizen et al. 2002), [28]Jiang and Gibbs (2005).

In this context the potential for far-field effects of a shellfish farm or farms in a given system becomes a question of proportion of scales: the scale of the farm to the scale of the system, modulated by the oceanographic characteristics of the system. The application of scaling concepts to assessment of potential far-field effects has several consequences.

In small bays, fjords or estuaries, ecosystem boundaries are relatively easy to define. This is more difficult for open coast or offshore installations. Appropriate definition of system boundaries is however, critical to properly assessing, predicting or measuring the environmental effects in such systems. Because the potential for effects is determined by the proportion of farm to system, selection of too large a system boundary will ensure that no effects can be expected or observed. Selection of an inappropriately small area may either magnify the potential effects (if boundaries are considered to be closed) or trivialize them if export or passing beyond system boundaries makes them "somebody else's problem". In contrast, such concerns about boundaries are minimized if spatially

explicit models are used as the selection of appropriate boundaries just must be beyond the zone of influence of a farm.

Shellfish farms come in many sizes. In some places a single lease may take up an entire system while in others multiple leases or types of leases may occupy a system. Unless there are location specific hydrodynamic characteristics that influence overall system behaviour, cumulative effects of multiple farms may be similar to effects of a single large farm. Several important points can be derived from this. Firstly, it is the amount and intensity of farming within the system that is utilized or occupied by shellfish farms that is the variable of interest here and not the number of farms. Secondly, effects resulting from increasing numbers of shellfish in a system are not necessarily additive or even monotonic. Thirdly, a single farm in a multi-use system cannot be considered in isolation. It is the overall effect of shellfish added to the system that will determine the potential for far-field or ecosystem-scale effects. In this synthesis therefore, they are treated together. Cumulative effects of shellfish aquaculture and other human activities will depend on both the effects of each activity under consideration and the potential for synergistic or antagonistic effects. The cumulative effects of mussel aquaculture and terrestrial agriculture are presented here as a case in point.

FACTORS THAT CONSTRAIN ECOSYSTEM SCALE EFFECTS

Productivity of coastal systems is frequently limited by inorganic nutrient supply and/or by habitat availability. Bivalve aquaculture affects system behaviour by shifting these critical limitations. The farms add or modify substantial amounts of habitat. Rope, raft and rack culture adds hard substrate often above compensation depth in the upper water column thus creating additional habitat for sessile fauna and flora. In-beach and on-sediment culture modify the sediment grain size and often affect the hydrodynamics of the benthic boundary layer (Miller et al. 2002b). Bivalves also alter inorganic nutrient fluxes directly via excretion and indirectly as they increase seston deposition rates, enhance remineralization and denitrification and reduce microphytobenthos production. The end result of these system modifications in terms of ecosystem scale effects will depend on the physical characteristics of the system and the relative size of the farm.

The potential for environmental effects of aquaculture activities at the system level is to a large degree determined by the physical characteristics of the system. The hydrodynamic regime in concert with the bathymetry and shoreline morphometry, influence available habitat, primary productivity, community structure and distribution, secondary productivity and the behaviour and transport of particulate matter. Seston supply in particular is regulated by advective processes (import and export), sedimentary losses and in situ production. Coastal geomorphology, fetch, exposure and bathymetry will influence benthic habitat types, the balance between sedimentation and resuspension and the distribution of erosional vs. depositional substrates (Wallin and Håkanson 1992). Wind, currents and freshwater outflow

govern nutrient inputs, losses and sequestration and thus set limits on primary production.

In estuaries, freshwater outflow dynamics are influenced by discharge, hydrography and topography of the coastal environment (Ardisson and Bourget 1997) and will in turn influence horizontal transport and water column stability. As well, the coupling between estuary and coastal ocean will also influence the dynamics of estuaries. This is particularly important in systems where the primary source of nutrients comes from the ocean (Hickey and Banas 2003). While there is not often a direct relationship between primary productivity, nutrients or inflow/outflow and secondary productivity in coastal systems (Ardisson and Bourget 1997; Estevez 2002) the relationship becomes apparent once habitat availability is taken into consideration. For example, fish stock productivity in Texas estuaries has been related to freshwater outflow in combination with habitat availability and temperature (related to faunal development rate) (Estevez 2002). Such relationships indicate that the interactions between habitat availability (a function of geomorphology, hydrodynamic regime and bathymetry) and nutrient supply (a function of advection, remineralization, mixing regime, etc.) are key factors determining secondary productivity.

In coastal regions nutrient supply is largely dependent on the interaction between currents and bathymetry. On coasts with a broad shallow continental shelf nutrient supply will be dominated by onwelling onto the continental shelf and the outflow of rivers while for coasts with a narrow shelf, currents and wind-driven upwelling and downwelling will determine nutrient supply at the large scale (Hickey and Banas 2003). Primary production and the productivity of mussel farms in the Rías of Northwestern Spain have been related to nutrient supply by upwelling events and downwelling export of blooms that are dependant on seasonal wind and current direction (Figueiras et al. 2002). At intermediate scales bathymetric features such as banks and submarine canyons will also influence nutrient supply due to interception, acceleration or modification of current fields and the creation of gyres that can retain particles that would otherwise be exported (Hickey and Banas 2003).

THE IMPORTANCE OF SCALE

The concept of scale as an important determinant of ecological pattern has arisen in parallel with the emergence of landscape ecology as a discipline (Schneider 2001). For a recent discussion of the importance of scale and temporal and spatial heterogeneity for benthic ecology see Raffaelli et al. (2003) and Solan et al. (2003). Two important concepts are pertinent. Ecological processes operate within a hierarchy of scales (Weins 1989; Pech et. al 2002; Parry et al. 2003; Brind'Amour et al. 2005), and small scale studies or patterns do not necessarily scale up to larger areas. Thus the question of interest must be matched to the relevant scale, and the methodologies employed must be appropriate to

measurement at that scale. If question and scale do not match then we risk extrapolating beyond the limits of the patterns or relationships uncovered.

When dealing with ecosystem scale consequences of human activity the potential for effects will depend on the relative sizes of activity and ecosystem. Thus it is the proportional size of farm to the ecosystem that will determine the potential for observable environmental effects and their magnitude. The effect if any, of a small farm in a large bay may be below the detection limits of current techniques whereas the effect of a large farm in a similar sized system may be readily observable as would the effect of the small farm in a small bay. Therefore any determination of the potential for ecosystem scale effects must be made in the context of the ratio of farm size to ecosystem.

SCALING ANALYSIS

In organismal biology, ratios are considered to be biologically meaningful properties of organisms and are frequently used to explore relationships of structure to function. Similarly, scaling arguments are frequently used in engineering and physics to relate properties to function (surface:volume ratio to heat loss for example). Ratios and scaling arguments are not so often used in ecology. This may in part be due to concerns about the statistical difficulties in dealing with ratios where both terms are measured with error. Scaling arguments are however very important in determining the size of effect that may be anticipated as a consequence of human activities in marine environments. The characteristic scales or rates of any potentially important processes are formed into ratios, and their relative magnitudes suggest which processes must be considered and which may be ignored (Miller et al. 2002a).

Ecosystem scale effects of shellfish aquaculture are anticipated only if the farm is large relative to the entire system. Figure 1 shows a schematic of this concept. As the size of the farm increases relative to the ecosystem, the magnitude of effect will also increase. At the observable effects threshold, the farm is large enough to measurably affect the surrounding environment and this effect increases as the farm size. The acceptable/unacceptable effect threshold will depend on the property(ies) of interest and the management criteria applied for that system. The property(ies) of interest will also determine the appropriate units for farm and system quantification. For example, they might be quantified in terms of surface area covered, shellfish biomass, secondary production, primary production demand (this latter would be appropriate in dealing with carrying capacity) or carbon or nutrient fluxes.

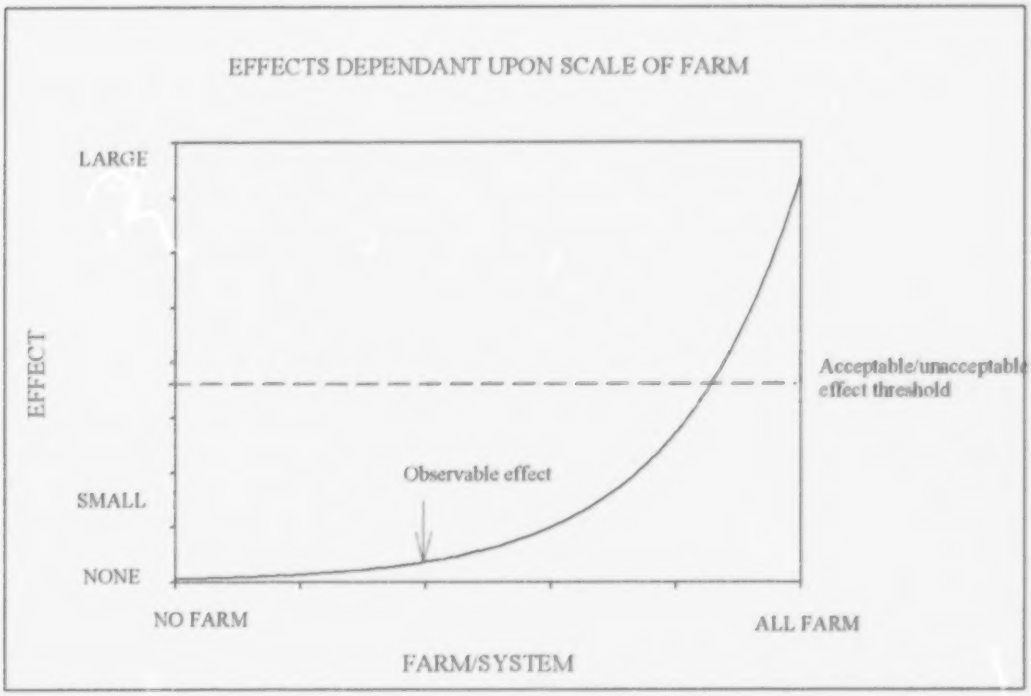

Figure 1. Conceptual diagram of how the ratio of the size of the farm to the size of the ecosystem might be expected to influence the magnitude and observation of effects. The observable effect level (arrow) is the point at which the effect becomes measurable. The acceptable/unacceptable threshold (dashed line) would depend on management objectives and criteria for the system.

PREDICTION OF POTENTIAL EFFECTS

The applicability and utility of several types of models for the prediction of potential far-field or ecosystem scale effects is examined in two modeling sections of the review by Chamberlain et al. (2006). Dowd evaluates a mathematical model to predict lower trophic level effects of shellfish aquaculture and Grant assesses the application of simple index models for prediction of various ecosystem properties of interest. In the larger literature there are numerous examples of ecosystem models applied to systems containing shellfish cultures. These often follow material or energy flow through small well defined systems like lagoons, fjords or small estuaries. While the approach and concepts behind this type of models are transferable they must be reparameterized for each system making generalizations difficult. Alternatives that can be applied more broadly can be found in the empirical models of Meeuwig et al. (1998) and Wallin and Håkanson (1992). In these observations from a number of systems are analyzed by regression to determine the best predictors of the variables of interest. Empirical models of this type are considered applicable to similar systems however, care must be taken not

to extrapolate beyond the range of the observations upon which the original models are based.

A further approach to predict far-field ecosystem effects is the use of mass-balance or food web models. Early conceptual mass-balance models examined the influence of bivalve culture as a part of the ecosystem (Tenore et al. 1982) but not as a model to predict the ecological productivity capacity (the stocking density that does not cause unacceptable ecological impacts, Inglis et al. 2000) of a system. More recently, a number of studies have used ECOPATH (Christensen and Pauly 1992) to determine the trophic functioning of areas that include bivalve culture in Chile (Wolff 1994), Taiwan (Lin et al. 1999), South Africa (Stenton-Dozey and Shannon 2000), Brazil (Wolff et al. 2000), and Italy (Brando et al. 2004). The complexity (i.e. number of trophic groups considered) and completeness of these models differ considerably. As could be expected, the presence of bivalve culture has typically been predicted to favour short energy pathways with high trophic efficiency and may contribute considerably to energy cycling in the studied systems. Unfortunately, the basic aim of these studies was not specifically to determine the ecological carrying capacities of the areas under consideration, although this was evaluated in some cases (e.g. Wolff 1994). A recent paper (Jiang and Gibbs 2005) specifically attempts to determine the carrying capacity of an area in New Zealand for bivalve culture using a mass-balance approach and the ECOPATH model. Interestingly, they found that although the production carrying capacity (the stocking density at which harvests are maximized, Inglis et al. 2000) of the area was 310 t yr-1, the ecological carrying capacity of the area was only was 65 t yr-1, above which point there would be major changes in energy fluxes within the system's food web. Future work is planned by Jeanie Stenton-Dozey (pers. comm.) to compile an ECOTROPHIC model of the Hauraki Gulf, New Zealand, to develop a sustainable fisheries and aquaculture industry in the region. It should also be mentioned that some work with mass-balance models has been directed at understanding the multi-species aquaculture at a bay-wide scale with reference to part of the surrounding ecosystem (macro-algae) (Nunes et al. 2003). This is pertinent to the Canadian situation as bivalve culture is often done in areas with more than one type of species being cultivated and macro-algae and macrophytes are a common dominant habitat in the surrounding area.

This approach does have its limitations. First, the models used are typically steady-state and thus temporal variation in processes may not be included. Second, the mass balance model typically used (ECOPATH) is not spatially explicit. Thus the model may not be used to differentiate between near-field and far-field effects. Third, an understanding of many biological parameters (life history values, interactions, etc.) is sorely lacking. And finally, this method typically only considers the ongrowing phase of the culture; other phases in bivalve culture (see outline of steps in McKindsey et al. 2006) also need to be studied and understood.

INDICATORS AND MEASURES OF FAR-FIELD EFFECTS

The environmental effects of bivalve aquaculture at local to ecosystem-wide scales have been reviewed and measures and indicators of these effects have been evaluated by Cranford et al. (2006).

CUMULATIVE EFFECTS OF SHELLFISH AQUACULTURE AND NUTRIENT ENRICHMENT FROM LAND-USE

Applications of agricultural fertilizer to farm lands enrich nutrient concentrations in surface and ground water. Upon reaching coastal systems, these nutrients stimulate plant growth and can disrupt the natural balance between the production and metabolism of organic matter. Although there are large differences in the inherent sensitivity of coastal regions to nutrient enrichment, eutrophication can be expressed as a complex suite of both direct and indirect responses to the change in nutrient inputs (Fig. 2).

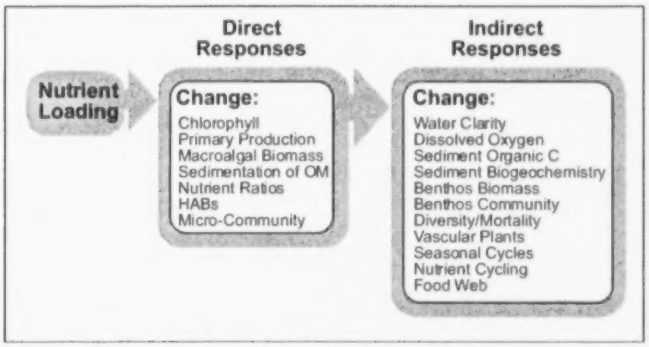

Figure 2. Schematic diagram of direct and indirect ecosystem responses to nutrient inputs from land-use (adapted from Cloern, 2001).

Concentrations of nitrogen and phosphorous in PEI estuaries increased substantially between the 1960s and 1990s and ten of 20 embayments sampled in 1998 and 1999 exhibited nitrogen levels exceeding the threshold for eutrophic conditions (DFO 2000). Nutrient loading in PEI, which has a relatively small population density, is largely due to agriculture. Meeuwig (1999) reported strong correlations between coastal nitrogen concentration and land-use (% agriculture area) suggesting a large influence of agricultural activities in many of the PEI embayments that are extensively leased for shellfish culture. Anoxic events due to the proliferation and decomposition of sea lettuce are also reported as becoming more widespread (DFO 2000).

The following discussion outlines the potential interactions between shellfish aquaculture and nutrient enrichment, with the intent of developing a conceptual model of the cumulative effects on fish habitat. The results of intensive field and modelling studies of a nutrient enriched and intensively leased embayment (Tracadie Bay, PEI) are used as a case study to show the impact of this anthropogenic interaction on the environment, and the consequences to fish habitat and shellfish aquaculture.

CUMULATIVE HABITAT EFFECTS OF SHELLFISH GRAZING IN NUTRIENT ENRICHED SYSTEMS

Unlike finfish aquaculture, external feed, which contributes to coastal eutrophication, is not used in shellfish aquaculture as practiced in Canada. In contrast, shellfish are widely reported to moderate the effects of nutrient enrichment through their grazing of phytoplankton biomass. Speculations that intense shellfish culture can affect coastal ecosystems in positive ways were first supported by observed changes in large estuarine ecosystems in which natural shellfish populations have either dramatically increased (e.g. San Francisco Bay: Cloern 1982; Officer et al. 1982; Alpine and Cloern 1992) or decreased (e.g. Chesapeake Bay: Newell, 1988). Both of these systems are highly eutrophic owing to intense farming and industrial/residential development within their watersheds. The filter-feeding shellfish are believed to mitigate negative effects of eutrophication by ingesting large quantities of microalgae and suspended particulate matter and thereby increasing the estuary's grazing control of excess phytoplankton biomass.

Indirect evidence indicating that the presence of large shellfish populations, wild and cultured, can play a key role in controlling coastal ecosystem responses to nutrient loading includes:

1) *Correlations:* Studies have noted significant inverse relationships between estuarine chlorophyll concentration and resident shellfish biomass (Kaas et al. 1996 as translated in Cloern 2001; Meeuwig; 1999) that imply a link between food supply and grazer.
2) *Shellfish grazing calculations:* Calculations of the amount of food filtered by shellfish populations and communities, based on laboratory-derived filtration rate models, indicate that shellfish can improve water clarity under nutrient enriched conditions (e.g. Cloern 1982; Officer et al. 1982; Newell 1988; Alpine and Cloern 1992).
3) *Experimental enclosures:* Additions of mussels at natural densities to large estuarine enclosure tanks reduce chlorophyll levels in tanks enriched with nutrients (Riemann et al. 1988, Prins et al. 1995).

The introduction of shellfish filter-feeders to eutrophic coastal regions has been widely promoted as a potentially valuable tool for mitigating the negative habitat effects of nutrient enrichment (e.g. Rice 2001). Shellfish aquaculture in nutrient

enriched systems has the benefit of not only controlling excess phytoplankton biomass, but also results in the removal of excess nutrients from the region in the shellfish harvest. These direct effects of shellfish aquaculture are represented in our first conceptual model of the cumulative effects of the shellfish/agriculture interaction (Fig. 3). This model focuses solely on bivalve grazing activities and on the potentially positive benefits to fish habitat via cropping of excess phytoplankton and removal of excess nutrients in the harvest. It should be noted that these positive effects of shellfish grazing in eutrophic systems can be reduced or lost if aquaculture intensity were increased to the point where food supplies become overly depleted and/or the nutrient extraction begins to affect natural coastal ecological processes.

This simplistic model of cumulative effects does not account for other potential habitat effects associated with bivalve feeding. These include impacts on water column phytoplankton communities resulting from the selective feeding behaviour of shellfish on relatively large (greater than 1-5 µm diameter) suspended particles. High levels of shellfish aquaculture have been observed to cause a change from primarily large (nanoplankton) to smaller (picoplankton) microalgal species (Olsson et al. 1992; Prins et al. 1998; Souchu et al. 2001; William Li, (unpublished data). Based on these observations, Newell (2004) suggested that bivalve grazing may adversely affect food quality for other filter-feeders. Shellfish grazing can also directly stimulate system primary production such that algal cell removal may be compensated by an increase in phytoplankton production. Mesocosm studies examining the role of the clam *Mercenaria mercenaria* in controlling seston concentration indicated that a relatively low abundance of clams doubled primary production and altered the community structure of the plankton (Doering and Oviatt 1986; Doering et al. 1989).

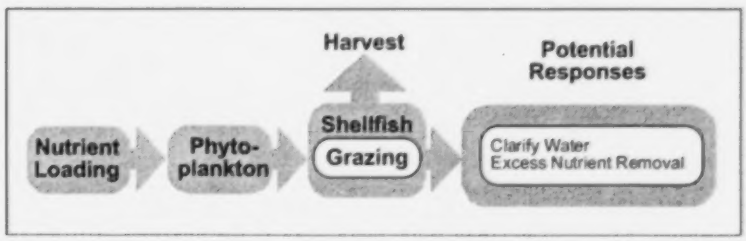

Figure 3. Schematic diagram of a simple conceptual model of shellfish aquaculture/ agriculture interactions, and the potential effects on coastal fish habitat.

Factors that may contribute to the observed shellfish-mediated optimization of primary production are; increased light through reduced turbidity (assumes algae

are light limited), greater growth of algae through continuous grazing of older cells, and a shift to faster growing algae species (Prins et al. 1995). Increased light can also allow nuisance species of macroalgae that grow in nutrient enriched conditions to become established. When present in sufficient quantities, they can cause sediment hypoxia when they decay. Bivalve grazing also affects food availability to other species, such as the zooplankton. Direct competition with, and ingestion of zooplankton can cause changes in zooplankton community structure and abundance (Lam-Hoai and Rougier 2001).

While the introduction of shellfish filter feeders can contribute to the moderation of eutrophic conditions in nutrient enriched estuaries, the cumulative effect of intense bivalve grazing on coastal ecosystems and fish habitat is obviously more complex than described in Fig. 3. Potentially opposing positive and negative habitat effects from shellfish filter-feeding are expected. Some of these interactions are detailed in an enhanced conceptual model of the cumulative effect of the shellfish aquaculture/ agriculture interaction (Fig. 4).

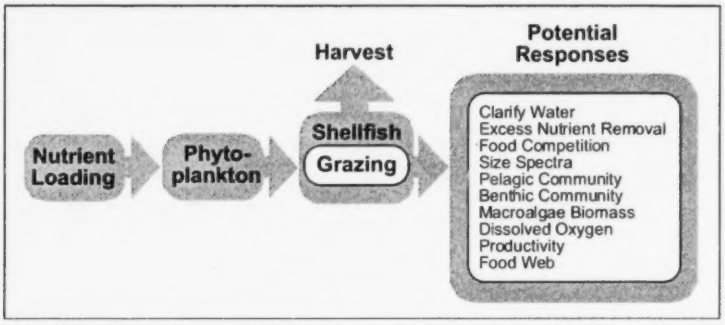

Figure 4. Schematic diagram of an enhanced conceptual model of shellfish aquaculture/agriculture interactions and the potential effects on coastal fish habitat.

HABITAT EFFECTS OF SHELLFISH BIODEPOSITION AND EXCRETION IN NUTRIENT ENRICHED SYSTEMS

The first two conceptual models of shellfish aquaculture/agriculture interactions are restricted to considerations of habitat effects related to the intake of excess phytoplankton by shellfish (Fig. 3 and 4). The biodeposition of organic matter in feces and the excretion of nitrogen are important consequences of bivalve feeding that also need to be considered in determining the net effect on fish habitat. Shellfish feces contain undigested organic matter and nutrients that could stimulate benthic microbial metabolism, alter sediment chemistry, and increase the probability that benthic communities will change (see Cranford et al. 2006). Benthic communities are highly sensitive to the organic enrichment effects of

eutrophication and the presence of shellfish aquaculture can compound these effects by channelling more organic matter to the seabed than would occur if they were not present. Although shellfish aquaculture can remove some of the excess organic matter from the system in the form of harvested tissue, they also feed on other internally produced and imported sources of living and detrital material. The shellfish mediate the rapid settlement of all these forms of suspended organic matter by ingesting small particles and producing large fecal pellets that settle at rates up to 40 times faster (Kautsky and Evans 1987).

The consumption and deposition of suspended particulate matter by farmed shellfish can play a significant role in controlling the amounts and forms of nitrogen in coastal systems, the retention of nutrients in the coastal zone, and the rate of nitrogen cycling (reviewed by Dame 1996). This biodeposition of feces provides a means of retaining nutrients in coastal areas where they are recycled within detrital food chains, rather than being more rapidly exported (Jordan and Valiela 1982). This focuses the negative effects of nutrient loading on this region. Benthic nutrient mineralization is increased at aquaculture sites as a result of the increased organic matter sedimentation, greatly increasing rates of nitrogen cycling (Dahlback and Gunnarsson 1981; Kaspar et al. 1985; Feuillet-Girard et al. 1988; Barranguet et al. 1994; Grant et al. 1995). Nutrient cycling rates and availability may also be increased in the presence of suspended culture through the mineralization of the large amounts of feces and pseudofeces trapped within the holding structures. This permits nutrients to be released at shallower, more nutrient depleted depths than occurs if the nutrients are regenerated in the sediments (Strain 2002). Asmus and Asmus (1991) suggested that the ability of mussel beds and culture sites to reduce the standing stock of phytoplankton through their feeding activity is unlikely to combat anthropogenic eutrophication because the shellfish also promote primary production and accelerate the turnover of phytoplankton through their effects on nutrient cycling.

The introduction of physical structures to marine environments causes a "reef effect" where the structures are used as habitat and where the shellfish and epibionts provide an additional food source for predatory and scavenger species (demersal fish and macrofauna). This may be viewed as a positive effect from a fisheries perspective if the predators are resource species. A major gap in knowledge is the cumulative effect on fish habitat or habitat productivity of increasing the abundance and/or productivity of attracted species, while simultaneously altering the community structure and/or reducing the productivity of some other resident species (e.g. benthic infauna effects from organic enrichment and particulate food competition).

An additional ecosystem consequence of bivalve aquaculture potentially stems from the transformation of some of the ingested particulate minerals into dissolved nutrients that are excreted. Excretion of ammonia by dense bivalve populations appears to exert a controlling influence on nitrogen concentrations in some coastal regions (Dame et al. 1991), including a mussel culture site in Nova Scotia (Strain

2002), and this aspect of bivalve culture may have a positive effect on the phytoplankton (Maestrini et al. 1986; Dame 1996). Excretion could also result in a change in the composition of the inorganic forms of nitrogen, resulting in increasing ammonium:nitrate ratios relative the natural ratios. Ammonium is preferentially utilized by the small pico-phytoplankton (Wafer et al. 2004) that are not efficiently grazed by shellfish. Ammonia is also an important nitrogen source for heterotrophic bacterial growth (Kirchman 1994). Thus, not only do shellfish selectively graze the larger phytoplankton forms, they also enhance the growth of the smaller forms through their excretion products.

Shellfish biodeposition and excretion and their related benthic organic enrichment and nutrient dynamic effects are included in our next conceptual model of shellfish aquaculture/agriculture interactions (Fig. 5). Tidal exchanges of natural food sources for shellfish are included in this model along with the excess phytoplankton as they all contribute to the shellfish food supply, and therefore to the cumulative habitat effects. This model emphasizes the fact that interactions in the coastal zone between farmed bivalves and nutrient loading are highly complex and all aspects need to be balanced objectively and integrated quantitatively before any conclusions can be reached regarding the net effect (positive or negative) of using shellfish aquaculture as a means of modulating coastal eutrophication trends.

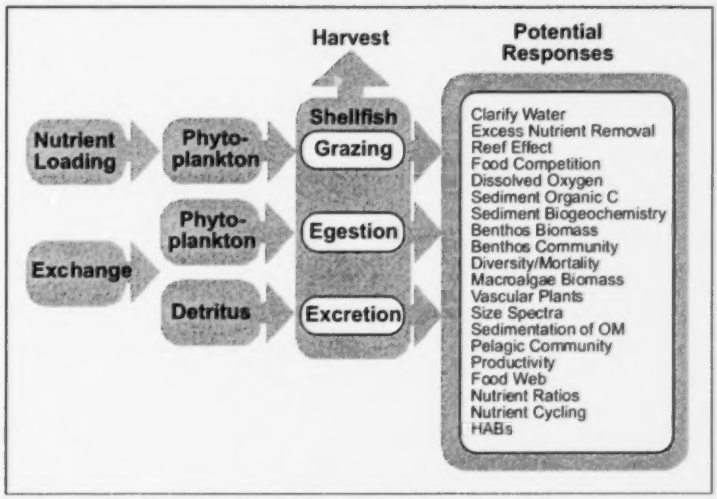

Figure 5. Schematic diagram of a comprehensive conceptual model of shellfish aquaculture/agriculture interactions and the potential effects on coastal fish habitat.

CASE STUDY ON SHELLFISH AQUACULTURE INTERACTIONS IN A NUTRIENT ENRICHED COASTAL BASIN: TRACADIE BAY, PEI

Recent multidisciplinary studies conducted by DFO, university and foreign scientists in the Tracadie Bay/Winter Harbour system (Fig. 6) have provided insights into the individual and cumulative effects of nutrient run-off from agricultural lands and extensive mussel culture operations. These data were used to critically evaluate the above conceptual models of shellfish aquaculture/agriculture interactions and to provide a real-world context to our discussion of potential cumulative effects on coastal fish habitat.

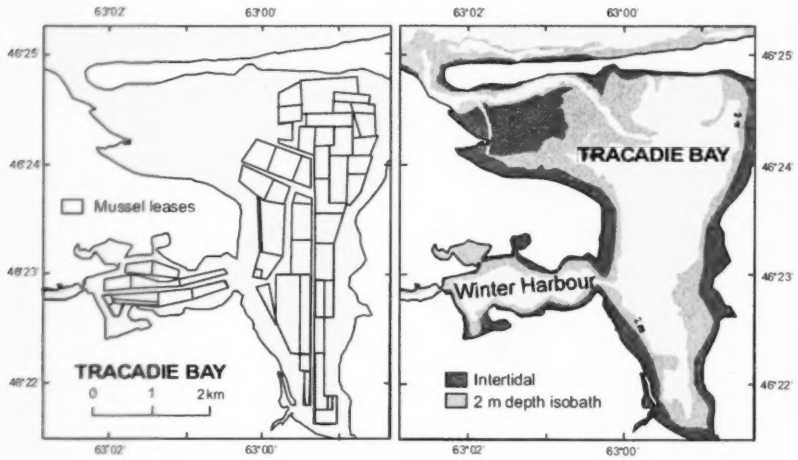

Figure 6. Maps of the Tracadie Bay/Winter Harbour system and distribution of mussel aquaculture leases. Winter River enters Winter Harbour on the left.

Nitrogen and phosphorous concentrations in Winter River, which drains a primarily agricultural watershed, are consistently high throughout the year (Strain et al. in preparation). The majority of these excess nutrients are utilized in the upper reaches of the estuary. Highest chlorophyll (phytoplankton) concentrations in the Tracadie Bay system are routinely recorded in Winter Harbour near the Winter River outflow (e.g. Fig. 6). Interactions between this agricultural enhancement of phytoplankton biomass and mussel aquaculture operations in this embayment were investigated through a combination of extensive field sampling (Cranford, in preparation) and ecosystem model predictions (Grant et al. in preparation). The model replicates major physical and biological processes in the bay and simulations were run using measured nutrient concentrations in Winter River, chlorophyll measurements outside the bay, and estimated density 10 mussels m^{-3} and distribution of mussel culture operations (Fig. 6). Model output was comparable with the observed magnitude and distribution of phytoplankton in Winter Harbour and Tracadie Bay (Fig. 7 and 8). Nutrient enrichment from agriculture run-off resulted in elevated phytoplankton biomass in Winter Harbour

while mussel grazing greatly reduced phytoplankton biomass in Tracadie Bay, compared with model runs without mussels. A high level of phytoplankton depletion within Tracadie Bay was predicted for all seasons, even when relatively high concentrations of phytoplankton enter the bay from the Gulf of St. Lawrence on each flood tide (Fig. 7: August; 325 mg C m^{-3}).

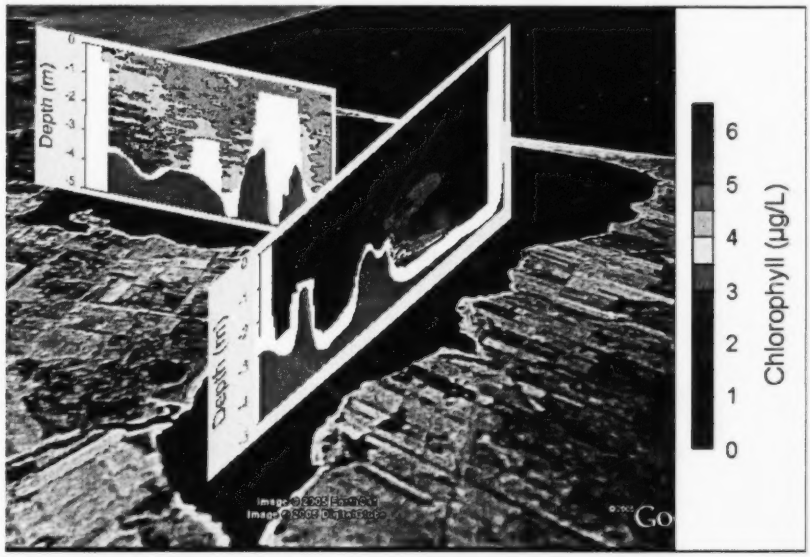

Figure 7. Distribution of chlorophyll in Winter Harbour (left) and Tracadie Bay (right) in summer (August 21, 2003). Note the relatively high concentrations in upper Winter Harbour, particularly near the outlet from Winter River (Cranford, in prep.).

Detailed maps of phytoplankton distributions in Tracadie Bay, obtained using data from the BIO-Acrobat towed vehicle (see Chamberlain et al 2006), provide evidence of the importance of nutrient-enrichment to mussel culture in Tracadie Bay, and confirm model predictions of bay-scale particle depletion. Repetitive sampling along a N-S transect in Tracadie Bay during different tidal stages (Fig. 8) shows a consistent pattern where high chlorophyll levels in Winter Harbour are transported into central Tracadie Bay on ebb tide, resulting in elevated levels in the mussel grow-out regions at low tide (Fig. 9). This food is rapidly consumed by the mussels, as is the food imported from outside the bay, resulting in depleted food concentrations in Tracadie Bay at high tide (Fig. 9).

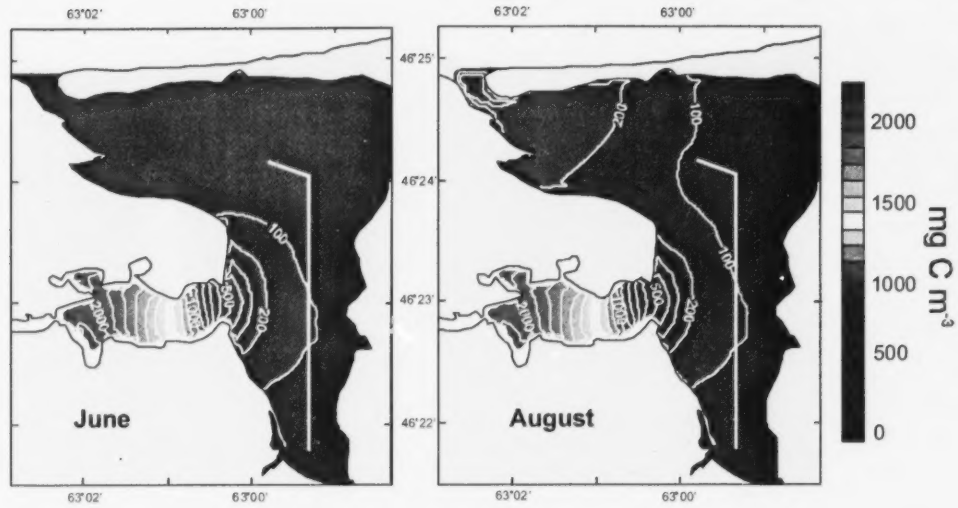

Figure 8. Predicted distributions of phytoplankton carbon (chlorophyll x 50) in Tracadie Bay during periods of low (June; left) and moderate (August; right) phytoplankton input from outside the bay and mussel densities in grow-out leases of 10 m^{-2} (Grant et al. in prep.). The yellow lines are the sampling transects referred to in Fig. 7 and 9.

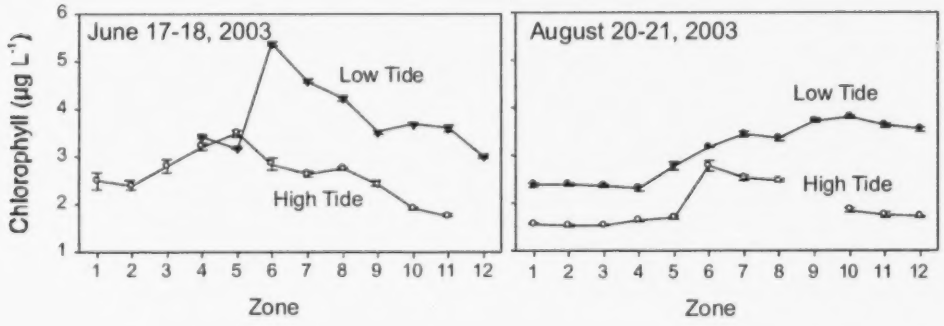

Figure 9. Average depth integrated phytoplankton carbon concentrations (±2 SE) along the north-south transect in Tracadie Bay (Fig. 5 and 7) in June (left) and August (right), 2003. The 12 geographic zones are spaced at 0.2' N latitude intervals, starting at 46° 21.8' N (Cranford, in prep.).

The combination of food supply mapping and ecosystem simulations provide ample evidence that intensive suspended mussel aquaculture in PEI can effectively remove excess phytoplankton from agricultural nutrient enrichment and thereby enhance water clarity. This assertion is compatible with all of our conceptual models (Fig. 3-5) of the cumulative habitat effects of these industries.

This "weight-of-evidence" approach also confirms that the current intensity of mussel culture in Tracadie Bay overcompensates for the effects of nutrient enrichment on phytoplankton biomass, resulting in bay-scale particle depletion. These results support industry observations of reduced mussel yields in this bay.

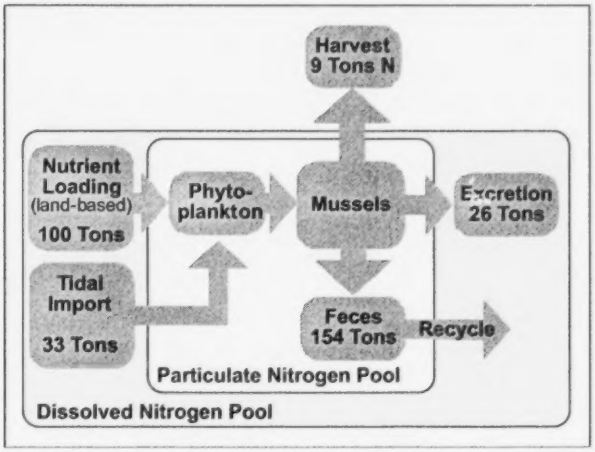

Figure 10. Major elements of the annual nitrogen cycle of Tracadie Bay, PEI, focusing on contributions from mussel aquaculture and nutrient loading from Winter River.

A nitrogen model was developed for Tracadie Bay to further investigate aquaculture effects on this system (Strain et al. (in preparation). As a starting point for this exercise, a nitrogen budget was developed to assess the magnitude of agriculture and aquaculture contributions to the nitrogen cycle (Fig. 10). Information collected on seasonal nitrogen (N) levels in Winter River indicates that approximately 100 tons of N enters this system annually from land run-off. Typical nitrogen export coefficients for different land uses suggest that approximately 75 tons of this input is agricultural in origin. In comparison, the annual harvest of mussels is approximately 9 tons of N (~0.5% of harvest weight is N). Even with the large area of this bay under culture, the harvested mussel biomass only extracts a small fraction of the excess nutrients added by agriculture. The suggested important effect of shellfish aquaculture on excess nutrient removal (Fig. 3-5) appears to be overestimated, at least in Tracadie Bay. In fact, the mussel culture directs much more of the available N to the seabed as feces than is removed in the harvest (Fig. 10). The predicted biodeposition of 154 tons N and excretion of 26 tons N by cultured mussels were calculated using published relationships between mussel size and their filtration and excretion rates (Smaal et al. 1997), and nitrogen absorption (digestion) efficiency (Figueiras et al. 2002). This simple N budget approach provides an indication of the significant role shellfish aquaculture can play in the retention and cycling of nutrients in coastal regions, as predicted in our contemporary conceptual model of cumulative habitat effects (Fig. 5). It should be noted however, that although the role of the biofouling community was not

included in this modeling exercise, it may represent an additional route of nutrient capture and sequestration (McKindsey et al. 2006) when macrofauna or flora make up a significant portion of the community biomass.

Insights into the structure and dynamics of pelagic communities under the intensively cultured conditions in Tracadie Bay were obtained from studies on bacteria and phytoplankton abundance, primary productivity and microbial community respiration measurements. (Harrison et al. 2005; William Li, unpublished data). Net primary production measurements in Tracadie Bay were consistently high for coastal basins at the latitude of Tracadie Bay with a timescale for phytoplankton growth that averaged 1 day. A production timescale of 2-5 days is typical for this latitude (Dowd 2003). Size-selective particle depletion by shellfish aquaculture in Tracadie Bay is likely responsible for some observed anomalies in the size structure of the microbial plankton community. Small picoplankton cells, which are not effectively retained by mussels, dominate the phytoplankton in Tracadie Bay and their abundance is remarkable when compared with global observations (Fig. 11A). The relatively high abundance of bacteria is also notable (Fig. 11B) and may be linked to reductions in natural bacteria grazers by shellfish feeding.

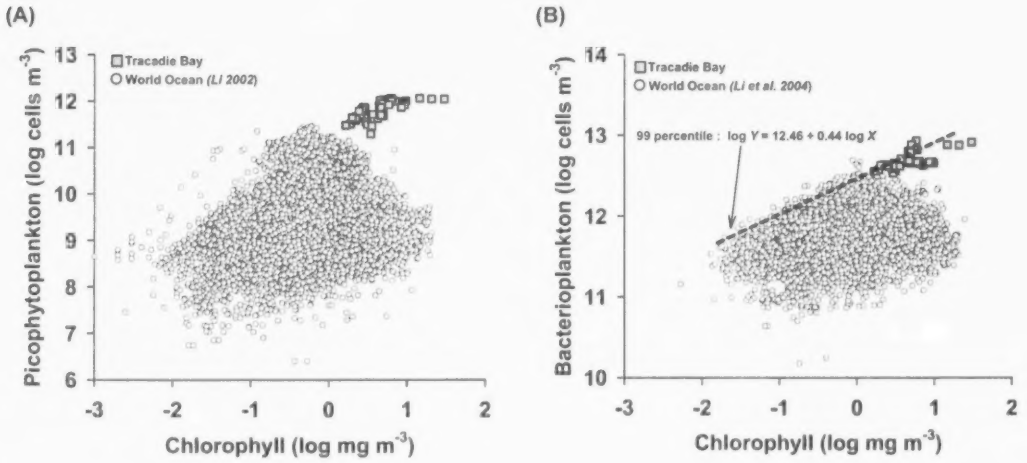

Figure 11. Plot of coastal and oceanic marine picoplankton (A) bacteria abundance (B) relative to phytoplankton (chlorophyll) abundance (W. Li, unpublished data).

The unique pelagic size structure and productivity measurements from Tracadie Bay are compatible with our contemporary model of the cumulative habitat effects of aquaculture and agriculture (Fig. 5). The high primary productivity and high picophytoplankton and bacteria abundance are consistent with the combined effects of nutrient enrichment and the predicted effects of shellfish, including: (1) optimization of phytoplankton growth; (2) size-selective particle depletion; (3)

increased water clarity (reduced light limitation); (4) retention of nutrients in the coastal zone; (5) increased ammonia (excretion) and nutrient availability; and (5) increased nutrient cycling rates.

Benthic habitat effects related to the large amount of organic material that is directed to the seabed in the form of feces (Fig. 10) were investigated in Tracadie Bay using benthic video and geochemical characterization of sediment oxic status. The results of a survey of sediment redox potential (Eh) and total sulfides (S) are shown in Fig 12. The Eh distribution map shows that the sediment organic enrichment effects in Winter Harbour are limited to a relatively small region near the Winter River discharge (Fig. 12). This region is only used for mussel spat collection and little additional organic enrichment impact from aquaculture is expected. Total sulphide levels in Winter Harbour are relatively low given the hypoxic nature of the sediment. This may result from the absence of sulphate in the freshwater at the head of the estuary.

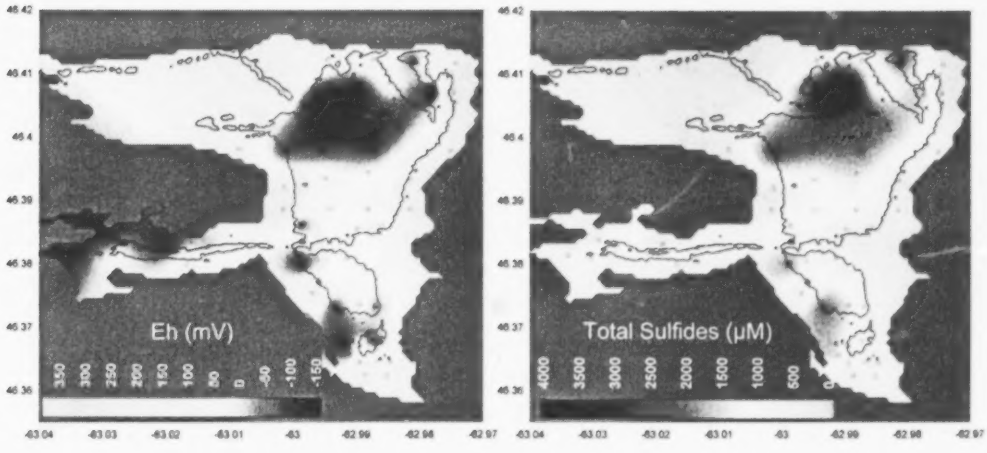

Figure 12. Redox potential (Eh; left) and total sulfides (right) distributions in Tracadie Bay in August, 2003. Sampling stations are indicated as blue circles and the 2 m depth contour is shown (Hargrave et al. unpublished data).

Sediments in deeper waters in northern Tracadie Bay are characterized as hypoxic by their low Eh and high S content (Fig. 12). The presence of sulphur-reducing bacteria mats on the seabed in this part of the bay indicates a high proportion of the seabed is anoxic. Since this area is outside the observed influence of land-based organic enrichment, biodeposition from suspended mussel aquaculture is implicated as the anthropogenic influence causing the impact. The biodeposition of organic matter by mussels has clearly resulted in hypoxic/anoxic conditions in receiving sediments, with the degree of impact related to both the distribution of mussel grow-out leases and local hydrodynamic conditions. Hydrographic patterns

within the Bay appear to result in a focusing of the benthic impacts of aquaculture on the northern part of the bay.

Owing to the ability to control phytoplankton biomass through grazing, intense shellfish aquaculture in Tracadie Bay has a large affect on coastal water clarity, while receiving a substantial economic benefit from the agriculture run-off. Phytoplankton produced on the nutrient run-off lessens natural food supply limitation to shellfish and increases the system *production carrying capacity* (optimum production level for the shellfish species). Assessments of *ecological carrying capacity* also focus on optimizing shellfish production, but take a more holistic approach to understanding all the effects of aquaculture on the environment and potential positive and negative feedback mechanisms. The weight-of-evidence provided by the use of a wide range of habitat indicators characterizes Tracadie Bay as an impacted coastal ecosystem in which the structure and function of benthic and pelagic communities has been significantly altered by the cumulative effect of anthropogenic activities, and particularly by the current high level of mussel aquaculture. While it is true that mussel aquaculture removes a fraction of the excess nutrients and organic production from agricultural inputs, shellfish aquaculture depends of the agricultural inputs as a food source for the mussels, and concentrates the eutrophication impacts of those inputs in the Bay.

RECOMMENDATIONS

A quantitative approach is recommended for assessing the *net* fish habitat impacts of shellfish aquaculture and other human activities. It would require a considerable effort to conduct extensive multidisciplinary studies, such as those conducted in Tracadie Bay, for all aquaculture inlets. However, a similar combination of habitat characterization, based on community structure and ecosystem function indicators, and modelling is recommended where a preliminary risk assessment suggests that a significant alteration of fish habitat and the ecosystem is possible. This approach allows the known positive effects of shellfish grazing on excess phytoplankton from nutrient enrichment to be balance against other potential effects of aquaculture (e.g. Fig. 5).

RECOMMENDATIONS FOR FURTHER RESEARCH

1) How do we determine the appropriate ecosystem boundaries for consideration of far-field effects?

   Application of a scaling approach is predicated upon the appropriate selection of the system under consideration. For small bays, fjords and estuaries this is relatively straightforward. It is less so for large systems or open coasts.

2) Can ecosystem sensitivity to perturbation by shellfish aquaculture be determined using simple easily measured variables?

3) What are the key characteristics of coastal ecosystems that will determine system response to shellfish aquaculture? Are there categories of coastal systems that respond in similar ways such that response is predictable for the category?

4) Can intersystem generalities be developed using scaling analysis as a non dimensional basis of comparison among systems? Can the resulting information be used to predict environmental effects on an ecosystem scale

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